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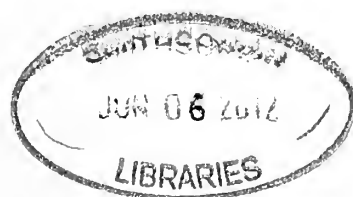
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**ARE BALDCYPRESS KNEES "ECOLOGICAL
ANACHRONISMS" EVOLVED TO DETER ROOT-TRAMPLING
AND OVERBROWSING BY NOW-EXTINCT MEGAFUNA?**

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ABSTRACT

Maryland and southern Delaware host the northernmost native stands of baldcypress (*Taxodium distichum*), a swamp tree, unusual in many ways, and unique by its enigmatic 'knees'. A new hypothesis accounts for these knees, growing vertically from lateral roots, as an ancient deterrent to trampling and root injury by large animals (megafauna, weighing 1 to 10 tons) in their quest for water to drink or escape summer heat. Almost all the most recent such megafauna became extinct about 13,000 years ago (ka). However, the genus *Taxodium* dates at least back to the Cretaceous (late Campanian; ca. 72-73 Ma), so the knees probably evolved long before the species of mammoths, mastodon and giant ground sloth present just prior to 13 ka. The knees may first have already evolved in response to dinosaurs, but no fossil knees predating the Plio-Pleistocene have so far been discovered. Because trees evolve slowly, they have not had time to adapt to the 13 ka megafauna extinctions. Thus, knees may be 'ecological anachronisms' with no apparent current function, in that respect similar to the apparently 'unnecessary' thorns on osage orange and honey locust, and the fruit of certain species, fruit rarely consumed and not readily spread by modern native fauna, such as the seed pods of honey locust and Kentucky coffee tree, the heavy Osage orange "horse apple", and many tropical examples (Janzen and Martin, 1982). Previous hypotheses for the origin of cypress knees (Briand, 2000-2001) may have failed simply because they assumed the knees have a modern function.

INTRODUCTION AND BACKGROUND

Maryland's botanic wealth includes some of the northernmost natural stands of baldcypress (*Taxodium distichum* var. *distichum*, the "trees with the knees"). Motivated by the continuing unsolved mystery on the origin and function of these knees (e.g., Briand 2000-2001), I here propose a new hypothesis: Baldcypress developed these knees as a deterrent to trampling and injury of shallow roots by large animals, such as mastodons, giant ground sloths, and mammoths, which would naturally, as cattle and pigs do today, seek out fresh water to cool themselves and quench their thirst. (The knees may have also served to protect young cypress from overbrowsing by megafauna). The hypothesis is hereafter referred to as the MRTD (**Megafauna Root-Trampling Deterrence**) hypothesis.

Although extensively logged, some Maryland cypress still exist and are partly preserved, albeit mostly as second-growth, in Calvert County (Battle Creek Cypress Swamp Nature Sanctuary) and on the Eastern Shore in Dorchester County (Blackwater National Wildlife Refuge), along parts of the Choptank, Nanticoke, Wicomico and Pocomoke rivers. The large Nature Conservancy Nassawango Creek Cypress Preserve is on a Pocomoke tributary, and at the Pocomoke's headwaters, in southern Delaware, baldcypress also grew and to some extent still grow in Trap Pond State Park (ca. 38.5° N), part of the Great Cypress Swamp.

Baldcypress stands out in the central and southeastern US forests as the only deciduous conifer (hence its name), its tolerance for swampy, intermittently flooded terrain, its rot and insect-resistant wood, its great dimensions (up to 3 meters (m) diameter and 40 m height), its flaring, buttressed base, and its longevity: old-growth baldcypress 400 to 600 years of age were once common (Muldoon, 1915), and a living 1700 year old cypress surviving along the Black River in southeastern North Carolina (Stahle et al., 1988) is easily one of the two oldest living tree species in eastern North America (The other species which may live to comparable ages (Larson, 2001) is the Atlantic white cedar (*Thuja occidentalis*). Baldcypress growth rings have proven invaluable for dendrochronology: annual growth rings are sensitive to growing season droughts, not because root moisture is in short supply in swamps, but because rain delivers oxygenated water and nutrients to their roots (Stahle & Cleaveland, 1992).

None of these remarkable characteristics, however, trump the unique cypress "knees"- vertical growths, resembling wooden stalagmites in appearance, and

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rising typically 0.5-1 m, rarely > 2 m from the shallow lateral cypress roots. What is the origin and function of these knees? Briand (2000-2001) quotes an early observer, Francois Andre Michaux, who in 1819 observed that “No cause can be assigned for their existence.” Despite nearly two centuries of speculation and even experiments—summarized below—there is still no consensus.

Briand (2000-2001) ends his review of cypress-knee function hypotheses with the suggestion that the knees may have “evolved in response to past environmental pressures that no longer exist, in which case their function may be lost in the depths of time”. I propose that Briand was right about the past environmental pressures, but that perhaps their original function can still be retrieved from the depths of time.

Beginning with the research of D. Janzen in tropical Costa Rica (Janzen and Martin, 1982), botanists and ecologists have begun to identify “ecological anachronisms”—plant characteristics that make no sense and appear to serve no function (Brounaugh, 2010). Janzen focused on plant reproduction—for example fruits that are not readily consumed by modern animals, or are simply too big: Were these fruits perhaps consumed and spread by animals that no longer exist? Many species of North American animals, many huge (notably mammoths, mastodons, giant ground sloths, short-faced bears, woodland muskox, giant beaver, stag-moose, camels, llamas, and horses—see Martin, 2005) disappeared from the Americas in the late Pleistocene, with latest data (see e.g. Kennett et al., 2009) placing the extinction date around 13,000 calendar years ago, commonly shortened to 13 ka (kilo-annum). Tree evolution has simply been much too slow to ‘catch up’ to the absence of megafauna—hence the term ‘anachronism’.

Of the three species native to the continental US, the Osage orange (hedge apple; horse apple; *Machura pomifera*) is native to a limited belt from southeastern Oklahoma southwards into eastern Texas), but actually thrives elsewhere and was widely planted in the 19th century as wind breaks and cattle fencing over much of the central and eastern US, including Maryland. So why does it not grow there naturally? The heavy, grapefruit-sized fruit is rarely consumed by modern species and basically can only roll downhill—how could a tree evolve such an inefficient reproduction strategy? The only plausible answer is that the ‘hedge apples’ were consumed by large, now-extinct herbivores such as mastodons and extinct Pleistocene horses, the small undigested seeds expelled with fertilizing dung, perhaps miles away. The fact that horses, which evolved in North America, relish Osage orange fruit suggests their ancestors did as well.

Moreover, Osage orange, along with honey locust (*Gleditsia triacanthos*) and some other species, are armed with numerous long spines, far more and higher up than needed to deter browsing white-tail deer. Why expend the energy to produce such spines if they are unneeded? Again, giant, now-extinct browsing animals seem to provide the answer—particularly the giant ground sloths, some of which could, while standing on two feet and supported by a thick tail, claw down branches up to more than 6 m above the ground, out of reach of other herbivores (Martin, 2005).

The **Megafauna Root-Trampling Deterrence hypothesis** posits that cypress knees are another such "ecological anachronism," evolved to deter large but now extinct animals, in their quest for drinking and, in hot weather, cooling water, from stepping on and injuring the lateral cypress roots to which the knees are attached. While stagnant swamp water was probably not ideal, many cypress swamps, or even just narrow riparian belts, border permanent flowing streams or rivers, so animals accessing such open waters still had to deal with baldcypress.

Due to low oxygen levels in swamp sediments, baldcypress, along with other swamp species, are forced to develop shallow root systems. In fact, "the fine feeder root system of cypress trees often congregate near the surface just below mean water level of the swamp" (Stahle et al., 2005, p. 16). Such feeder roots would be especially vulnerable. In addition to root injury, megafauna would harm the root system by compressing the soil around the roots—a recognized problem for modern living trees growing on dry ground as well, with culprits including cattle and even humans. Some animals may have learned to navigate through cypress swamps by stepping over or between the knees, thus avoiding injury to the underlying roots from which the knees grow, but soil compression would still occur. Because most or all of the "root trampling" creatures were herbivores, slow progress stepping around or over knees would make them, especially juveniles, more vulnerable to faster, smaller predators, such as sabre-tooth cats. Finally, younger cypress stands would still have foliage within browsing reach, so the knees may have served to defend young foliage. Baldcypress as young as 12 years may develop knees (Briand, 2000-2001), and at that age, the foliage is clearly still within reach of browsers. Newsome and Muhlbacher (2006) showed from dung analysis that late Pleistocene mastodons browsed extensively on baldcypress.

Previous hypotheses for the function of cypress knees.

Briand (2001) has most recently summarized the ca. half dozen hypotheses put forward in the last ca. 150 years to explain the function of cypress knees. The

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following is a brief list of these hypotheses, and the problems with each, as extracted from Briand's publication and in the order discussed by him. Depending on the hypothesis, the problems include: 1. lack of observational evidence, or even observational counterevidence; 2. absence of experimental verification attempts; and, 3. where tests have been attempted, negative or inconclusive results. See Briand (2000-2001) for references.

The **aeration hypothesis**, often popularly cited essentially as proven, posits that knees are a form of pneumatophores, or breathing roots such as occur on certain mangrove species. However, experiments on baldcypress knees showed oxygen uptake to be low; moreover, anatomical examination showed knees to lack the aerenchyma to transport air from the knees to the rest of the root system. Finally, the aeration hypothesis cannot explain why knees are rare or absent in deeper water. The MRTD hypothesis accounts for the negative experimental evidence for aeration. Moreover, megafauna wading out into deeper water, if they did so at all, would be at least partly buoyant, thus exerting little or no pressure on cypress roots, thus lessening the need for knees. The lack of knees on most cypresses growing on dry ground is consistent with both hypotheses.

Another hypothesis proposed that cypress knees serve to **vent biogenic methane** from swamp sediments, but this was disproven experimentally. The possibility that the knees play some role in **vegetative reproduction**, as root suckers do on other species, can be dismissed by the total lack of observational evidence. Frequently cited as a plausible explanation is the **mechanical support hypothesis**, according to which the shallow-rooted baldcypress develops knees to help stabilize the tree against windthrow. Because many knees grow vertically up from the junction of the lateral and vertical (downward) roots, the knees would add strength to these junctions. While this is perhaps the most plausible of existing explanations, observations show that knees can also grow from lateral roots where no junction exists, and junctions occur without knees above them. Moreover, this hypothesis, like aeration, does not account for the near absence of knees on trees growing in deeper water, where they would also be vulnerable to windthrow. In any case, experiments to test the difference between pulling down cypresses with knees and with knees removed have not been conducted (Briand, 2001). The **nutrient acquisition hypothesis**, that knees act as "drift catchers" to trap organic matter (i.e., nutrients) floating through the swamp when water is in motion, has not been tested, but at best provides a secondary function, because water flow through many swamps is rarely fast, and in any case, mostly moves

around debris fallen from cypress trees (i.e., is already available in the swamp). The latest hypothesis (**carbohydrate storage**) postulates the knees are storage organs. While the demonstrated presence of granules (plausibly starch-storing organelles called amyloplasts) and, on the cut surface of knees, also starch, supports this hypothesis, the lateral and vertical cypress roots were not similarly tested. Moreover, the hypothesis does not explain why knees rarely develop on cypresses growing in deep water or on dry land.

FOSSIL *TAXODIUM* AND THE LATE PLEISTOCENE (CA. 13 KA) MEGAFaUNA EXTINCTIONS

The geologically recent (ca. 13 ka) megafaunal extinctions, which turned North America into a "continent of ghosts" (Martin, 2005), is relevant to the MRTD hypothesis, but not because knees evolved in response to the species which became extinct then. In fact, the genus *Taxodium* originated prior to the evolution of large mammals, with the earliest occurrence (*Taxodium wallisii*) ca. 72-73 Ma, in the Late Campanian Horseshoe Canyon formation, Alberta (Aulenback and LePage, 1998) (L. Hickey, personal communication, 2011), so the knees may have evolved already during the time of, and in response to, dinosaurs. Well-preserved fossils show *Taxodium spp.* was widespread in the high Arctic at least from Late Paleocene until late Middle Eocene times, i.e., from about 57 to 43 million years ago (Yang et al., 2009).

Unfortunately the fossil record for cypress knees (in contrast to twigs, seeds, and pollen) is very limited. This is not surprising: living knees do not readily break off and float elsewhere, and once "dead" would decompose in place. Moreover, knees are sapwood, which rots much faster than baldcypress heartwood. The primary and perhaps only venue for knee preservation is rather rapid burial of living baldcypress swamps by sediment or volcanogenic debris. Examples of such buried swamps, including baldcypress stumps and knees, crop out (or formerly did so) along eroding bluffs of the Maryland Chesapeake Bay (Anonymous, 1906) and underlay a part of Washington, D.C. (Wentworth, 1924; Knox, 1966). The latter "Walker Cypress Swamp" comprised a ca. 1 m thick stratum ca. 6 m below street level in the area of the Mayflower Hotel and the new National Geographic building, but has largely been removed during construction. Other baldcypress parts have been found in Pleistocene deposits from New Jersey southwards (e.g., Berry, 1915), Virginia (Berry, 1909), North Carolina (Berry, 1907; 1926), and western Kentucky (a single twig; Berry, 1915). The only

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possible pre-Pleistocene knees are those described from the Citronelle Formation (Berry, 1916b), a widespread system of deltaic siliciclastic deposits extending from the central Gulf Coast to Florida. Although dating has long been problematic, more recent studies assigned the age of the Citronelle formation partly (Li and Meylan, 1994) or wholly (Cunningham et al., 1998) to the Pliocene. However, even the oldest known fossil *Taxodium* knees are less than 10% the age of the oldest known *Taxodium* fossils. Presumably the Plio-Pleistocene fossil *Taxodium* swamps date largely from warm interglaciations, although the “Walker Swamp” deposit under part of modern Washington, D.C. (Wentworth, 1924) may be only 55 ka (Marine Isotope Stage 3) in age (L. Hickey, personal communication, 2011), which if correct implies the species was present during climates cooler than modern.

Because knees are at least occasionally present also on the closely related species (or varieties) *Taxodium distichum* var. *imbricarium* (Pondcypress) and *Taxodium mucronatum* (Montezuma baldcypress, a species more prevalent on drier ground), and *Glyptostrobus pensilis* (Chinese swamp cypress), DNA might provide a minimum age for knee evolution, i.e., the age of the last common ancestor of these species. The formation of knees (albeit not as prolifically as on *T. distichum*; Metcalf, 1937) on the Chinese pond cypress (*Glyptostrobus pensilis*) (i.e., in another genus in the subfamily *Taxodioideae*) suggests an ancient origin for the knees unless the knees evolved separately. *Taxodium* spp. flourished in the high Arctic as late as 57-43 million years ago (Yang et al., 2009), but so did *Glyptostrobus* (which later died out in North America; e.g., Wittlake, 1970). Both genera coexisted during the late Cretaceous, so the common ancestor has to be older.

In any case, various kinds of megafauna have long coexisted with baldcypress and its ancestors- except for a few million years after the extinction of dinosaurs (ca. 65.5 Ma), when North America was emptied of all large land animals, and to some extent after 13 ka.. It is not inconceivable that the knees first evolved in response to dinosaurs (e.g., hadrosaurs, which inhabited swampy terrain), and have served the trees well ever since. However, a ‘dinosaur connection’ will remain very speculative until Cretaceous or at least Paleogene fossil knees are found, or until a comparably great age is estimated for the putative common ancestor of *Glyptostrobus pensilis* and *Taxodium distichum*.

Many of the late Pleistocene megafauna were descended from other large creatures, although some kinds (e.g. *Equus*) evolved into larger forms, plausibly

as a result of drying climates and resultant grassland expansion. The late Pleistocene megafauna are important for the MRTD hypothesis because their fossil record is much more complete, and their extinction is important as the basis for "ecological anachronisms" (e.g., Janzen and Martin, 1982; Martin, 2005; Bronaugh, 2010).

The latest Pleistocene megafauna extinctions have long puzzled scientists, with the abrupt, latest glacial climate changes and human overkill leading contenders. The great majority of genera, even most species, however, survived many earlier glacial ages and rapid deglaciations, with accompanying rapid climate and vegetation changes, from all evidence no different from the most recent ca. 18-10 ka deglaciation. The "overkill" hypothesis (Martin, 2005 and earlier publications) was based on the premise that numerous species of large American animals, having no previous experience with humans and slow to reproduce, were easily killed off. How spear-throwing stone-age humans could directly and indirectly drive such a large number and variety of genera (not just mammalian megafauna, but also birds) to extinction seems dubious, although man was certainly an extinction agent elsewhere (e.g., Madagascar, New Zealand, and Australia) at other times, even today (Martin, 2005). Moreover, the first human presence in the Americas has now been shown to predate by at least one or two millennia the ca. 13.5-13.0 ka Clovis Culture Paleo-Indians were long blamed, along with climate change, for the overkill. Problems with this simple 'overkill' extinction model are analyzed e.g., by Brook and Bowman (2002) and Barnosky et al. (2004). A more recent explanation attributes the extinction event to the impact and atmospheric explosion of a comet or cometary fragments 12.9 \pm 0.1 thousand calendar years ago (Firestone et al., 2007; Kennett et al., 2009). Although increasingly accepted, the comet impact hypothesis remains controversial (e.g., Kerr, 2010), as much of the adduced observational evidence was not replicated by others (e.g., Haynes et al., 2010; Daulton et al., 2010).

Pleistocene megafauna are often, at least in the media and among the public, associated with the last Ice Age, formally called the 'Wisconsinan' in the continental U.S. There is no evidence, however, that *Taxodium spp* grows or ever grew in glacial or periglacial venues, and animals native to such climates (such as the tundra-dwelling musk ox or the extinct woolly mammoth) would never have encountered a baldcypress swamp. Dating of buried logs, however, suggests cypress was growing at least as far north as 33.8 N in South Carolina ca. 25,000 years ago (Stahle et al., 2005), near the beginning of coldest part of the last glacial

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age. Calling Pleistocene megafauna "Ice Age" animals is misleading for two reasons: First, even during the most severe Pleistocene glaciations (about a half dozen, largely during the last half million years), numerous megafauna species inhabited the temperate and tropical Americas, including the natural range of the baldcypress and its ancestors. Second, both baldcypress and megafauna have a long history—many millions of years—in North America (e.g., Kurten, 1988), surviving numerous drastic climate changes with few extinctions. Those species that died out abruptly ca. 13,000 years ago were just the latest forms, those unfortunate enough to exist when the still mysterious "disaster" struck.

ANCIENT BALDCYPRESS PRESENCE IN MARYLAND

Both *Taxodium spp.* and megafauna have intermittently inhabited what is now Maryland and vicinity for a long time. The modern baldcypress swamps probably all date from or after the relative sea level stabilization ca. 7000-6000 years ago (e.g., Cronin et al., 2007)—allowing swamps to develop in coastal and estuarine venues. While *Taxodium* was probably absent during glacial climates, when boreal forests covered Maryland, a Pleistocene baldcypress swamp (mentioned above) flourished at the site of present Washington, D.C. Other Maryland Pleistocene baldcypress fossils, including knees, have been collected from buried swamps preserved in the Talbot formation at Bodkin Point, Grace Point, and Pond Neck (Anonymous, 1906). The latter site (39.42° N) shows that the natural range of *T. distichum* extended of the order 100 km further north during one or more warm Pleistocene interglaciations, compared to its historic range.

Much of the Maryland coastal plain is underlain by the Chesapeake Group, shallow marine sediments deposited from approximately 20 to 10 million years ago (most of the Miocene epoch), i.e., about 1000 times as far back in time as the megafauna extinctions. Fossils found in these marine strata include pollen, twigs and fruit (but no knees) of *Taxodium spp.* (e.g., Berry, 1916a), washed into the sea from nearby coasts, as well as fossil teeth of gomphotheres, an extinct elephant-like creature which plausibly browsed on *Taxodium* foliage.

BUT HOW TO TEST THE MRTD HYPOTHESIS, WHICH INVOLVES NOW-EXTINCT ANIMALS?

If the megafauna were still with us today, we could easily observe if mammoths, mastodons or giant sloths searching for water to drink or to cool off avoid knee-infested cypress groves. But, with North America now emptied of

most "suspect" species, direct tests are no longer possible. Cattle, horses and pigs, however, commonly, in the heat of summer particularly, wallow in shallow water, and their behavior could be observed, as could that of bison, one of the few surviving American megafauna. While baldcypress is not native to Africa or Asia, Old World megafauna similar to the large extinct American species might be observed in New World game parks where cypress swamps are present or their knees simulated. The Indian elephant is genetically closest to the mammoth (Martin, 2005), and might be the best test animal. The horse and camel families both evolved in North America, and surviving Eurasian species might still exhibit evolved avoidance of cypress knee-like obstacles.

Another approach might be to examine African swamp trees for other evolutionary adaptations to injury by modern African megafauna such as hippos, buffalos and elephants. As suggested by one of the anonymous reviewers of this paper, the knee-like root structures of mangrove (various species) and red maple (*Acer rubrum*, a common swamp companion to baldcypress) may also have evolved in part as a defense against large browsing animals.

Testing the shallow lateral baldcypress roots for vulnerability to injury from objects similar to megafauna feet—for example the long, sharp claws of giant ground sloths—might provide clues. According to Stahle et al. (2005, p. 16; see also Stahle and Cleaveland, 1992), to satisfy the trees' need for oxygen in still, stratified swamp waters and mud, generally hypoxic or anoxic at shallow depths, "the fine feeder root system of cypress trees often congregate near the surface just below the mean water level of the swamp" and are exposed to the air during droughts. Perhaps these fine feeder roots also provided food for some animals—a kind of vegetarian soup, another asset the knees might have evolved to defend. The knees themselves appear robust, but creative biomechanical tests could quantify their breaking strength if stepped on or tripped over by 1-10 ton animals. While sharp-tipped knees would be more painful to animals, the sharp tops may have been too easy to break off, hence easily damaging the cypress tree itself.

In the end, however, the "megafauna root-trampling deterrent" hypothesis is mainly a default hypothesis, deriving most of its promise from the failure of explanations previously advanced. C.H. Briand (2000-2001) may thus be proven "spot on" when he concluded that "The truth may be that cypress knees evolved in response to past environmental pressures that no longer exist." If the knees indeed turn out to be 'ecological anachronisms', they will join the ranks of Osage orange fruit and the thorns and/or large seed pods of honey locust and Kentucky coffee

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trees, as well as many tropical American flora (e.g., Janzen and Martin, 1982). In fact, baldcypress knees might be considered giant equivalents of honey locust spines, which evolved to deter browsing and the knees evolved to deter trampling.

As the millennia pass, if the Megafauna Root-Trampling Deterrence hypothesis and Darwin are correct, *Taxodium distichum* might thus eventually lose its now unnecessary knees. After all, a baldcypress growing on dry land already "knows" how to avoid investing energy to grow knees. Thus, whatever gene or genes are involved in triggering knee development on submerged roots may be turned off in some specimens, which then would survive to outcompete specimens still bothering to grow knees. On the other hand, it may turn out that the knees still perform additional, if only secondary functions, yet to be demonstrated, for their owners.

In any case, the 200 year long debate (Briand, 2001) over the origin and function (or functions!) of cypress knees will no doubt continue. Because knees form on both *Taxodium distichum* and *Glyptostrobus pensilis*, their common pre-Late Cretaceous ancestor probably had knees as well. If true, this would support knee evolution as a deterrent to trampling and browsing by dinosaurs. A concerted effort should thus be made by geologists to search for comparably old fossil knees, most likely preserved in swamps, buried by sediment or volcanogenic debris. However, of the four knee-producing *Taxodioideae* (baldcypress, Montezuma cypress, pondcypress, and Chinese pond cypress) only *T. distichum* is a prolific knee-producer and thus effective as a megafauna deterrent. This leaves the MRTD hypothesis open to the possibility that knees had yet another ancient function, which only *T. distichum* utilized in more recent geologic times to deter mammalian megafauna.

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**A CRITICAL CHECKLIST OF THE DECAPOD CRUSTACEA
(ARTHROPODA: DECAPODA) OF THE ATLANTIC COASTAL
BAYS OF MARYLAND**

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ABSTRACT

Records in the peer-reviewed and “gray” literature were collated and revealed the presence of 47 species of Crustacea in the order Decapoda distributed among 2 suborders, 20 families, and 31 genera in the Atlantic coastal bay system of Maryland. Comparisons of these fauna with that of the nearby Delaware and Chesapeake bays demonstrated greater internal similarity between those communities but little similarity between the faunas of those estuaries and the Maryland coastal bay system.

INTRODUCTION

Several faunistic studies of the macroinvertebrates of the Atlantic coastal bay systems of Maryland have been conducted for a variety of reasons. Lebber and Lipson (1970) and Drobeck et al. (1970) conducted benthic invertebrate inventories of the Sinepuxent-Chincoteague Bay system (Fig. 1) as a baseline examination of the fauna of the newly established Assateague Island National Seashore. Casey and Wesche (1982) examined the benthic invertebrates of the Assawoman-Isle of Wight-Sinepuxent Bay system as part of larger longitudinal studies, primarily of finfish, of the entire coastal system performed for the Tidewater Division of the Maryland Department of Natural Resources. Casey and his colleagues went on to report on a variety of studies examining the *Callinectes sapidus* fishery of the Maryland Atlantic coastal bays (Casey and Daugherty 1989; Casey et al. 2001a, b, c, d). Chaillou et al. (1996) sampled the Atlantic coastal bays of both Delaware and Maryland for the U.S. Environmental Protection Agency as a part of the Coastal Bays Joint Assessment made during 1993 the results of which were to be used in a study to relate land use to ecological conditions in these bays. Counts and Prezant (2002) examined the nearshore benthic invertebrate fauna of Assateague Island National Seashore as a part of an intensive quantitative and qualitative longitudinal study on benthic diversity and abundance in the waters surrounding the Maryland portion of Assateague Island.

Lists of species of decapod Crustacea that might be encountered along the Atlantic coast of Maryland can also be assembled from various field guides to coastal fauna (e.g., Gosner 1971, 1978; Meinkoth 1994). Other than providing a broad zoogeographic range, however, these guides provide no exact information concerning the Maryland coast. The agency reports (e.g., Casey and Wesche 1982; Chaillou et al. 1996; Counts and Prezant 2002) provide more exact information of the occurrence and distribution of the Decapoda but these are difficult to obtain and, other than the report of Counts and Prezant (2002) do not interrelate previous findings with the study reported. Hence, no critical list of the decapod Crustacea of the Atlantic coastal system of Maryland has been published in either the "gray" or peer-reviewed literature.

Our study reports the species of shrimp and crabs (Order Decapoda) that have been collected and reported by Drobeck et al. (1970), Leber and Lippson (1970), Casey and Wesche (1982), Chaillou et al. (1996), and Counts and Prezant (2002) and combines them with additional data provided by the Maryland

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Department of Natural Resources, Fisheries Service, to construct a critical list. This list is not intended as an ecological review of the Atlantic coastal benthic invertebrate macrofauna but rather a review of the occurrence and distribution of these organisms as revealed by three decades of collection on the coastal bay system of Maryland.

METHODS

Data Sources. Information on the identification and distribution of decapod Crustacea in the Atlantic coastal waters of Maryland (Fig. 1) was collated from the reports of Drobeck et al. (1970), Leber and Lippson (1970), Casey and Wesche (1982), Chaillou et al. (1996), and Counts and Prezant (2002). Additional data were obtained from fisheries reports (Cargo, 1959; Boynton, 1970), theses (Weissman, 1994), Maryland Department of Natural Resources, Fisheries Service reports (Casey and Daugherty, 1989; Casey et al., 2001a, b, c, d), and personal communications (Patton, 2002; Doctor, 2004). Comparisons of Maryland coastal decapods were made with those species listed for Delaware Bay (Watling and Maurer 1973) and Chesapeake Bay (Lippson and Lippson 1997).

Sampling Stations. Historical sampling stations are not always well described in reports and are usually indicated only as dots on a map. Drobeck et al. (1970) reported sampling 21 to 22 stations at each of three proposed dredge sites at Assateague Island at Pope Bay (22 stations), Fox Hill Levels (21 stations), and North Beach (21 stations). All of these sites are a part of Chincoteague Bay. Additionally, they sampled 64 stations in Chincoteague Bay proper. Each station of 1 m² was sampled using an escalator harvester, which collected all epibenthos and infauna present to a depth of 1 cm. Leber and Lippson (1970) sampled 156 stations in Chincoteague Bay, many of the stations being arrayed in cross-bay transects separated by 2.4 km. The study of Chaillou et al. (1996) reported sampling from 15 stations in Assawoman Bay, 17 in the St. Martin's River, 6 in Sinepuxent Bay, 19 in Newport Bay/Trappe Creek, and 36 in Chincoteague Bay. They did not, however, provide exact localities other than the generalized name for the coastal bay sampled.

Casey and Wesche (1982) were more detailed in the description of their sampling stations. They sampled from a total of eight stations distributed in Assawoman, Sinepuxent, and Chincoteague bays and provided comments on submerged aquatic vegetation (SAV), water depth, emergence, and substratum composition. Their sites, with original designations, were: Site 6, southeast side of Maryland State Route (MDSR) 90 bridge, Isle of Wight Bay-Assawoman Bay

system; Site 9, south of Drum Point, Assawoman Bay, near the Lighthouse Sound Country Club; Site 16, northwest side of Ocean City flats; Site 17, south side of Ocean City, Assawoman Bay, near Ocean City Inlet; Site 25, 100 m west of the Worcester County pier at Public Landing, Chincoteague Bay; Site 30, 200 m west of Inlet Slough, Assateague Island; Site 41, at confluence of Turville and Herring creeks, Isle of Wight Bay; and Site 42, 100 m inside an undeveloped bulkheaded dead-end canal off Manklin Creek, draining directly into the southern reach of Isle of Wight Bay.

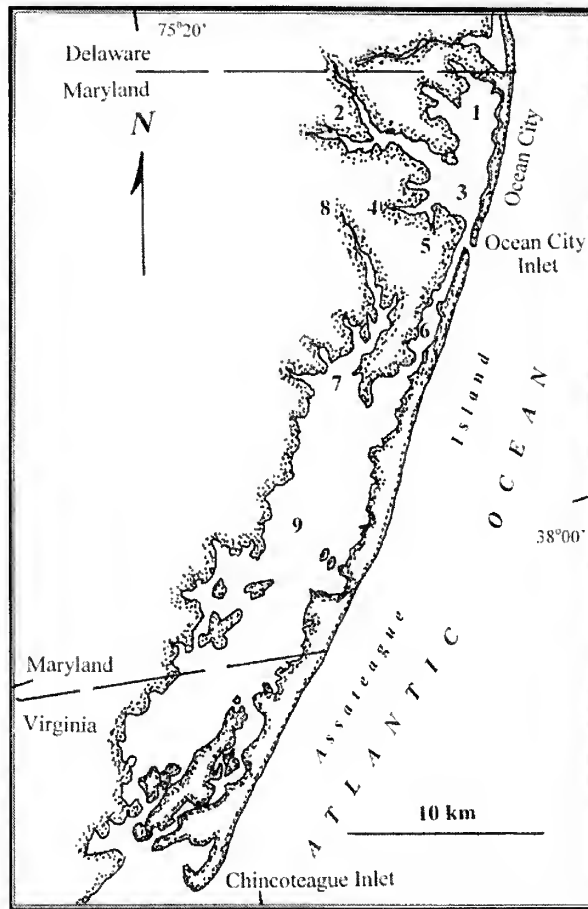


Fig. 1. Atlantic coastal bay systems of Maryland. Key to embayments: 1 = Assawoman Bay; 2 = St. Martins River; 3 = Isle of Wight Bay; 4 = Turville Creek; 5 = Herring Creek; 6 = Sinepuxent Bay; 7 = Newport Bay; 8 = Ayres Creek; 9 = Chincoteague Bay.

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The Assateague Island National Seashore Benthic Invertebrate Diversity (ASIS) Study (Counts and Prezant 2002) collected qualitative and quantitative samples. The study used 16 transects which cut across the island. Transect 1 was located 1 km south of Ocean City Inlet and each succeeding transect was separated by 2 km. Four ocean-side (nos. 2, 7, 12, and 16) and twelve bayside (Nos. 1, 2, 3, 4, 7, 8, 9, 10, 13, 14, 15, and 16) transects were sampled. Ocean-side transects were sampled at the swash zone, 5 m and 25 m offshore. Bayside transects were sampled at depths that included the swash, 0.5 m, 1.0 m, and 1.5 m based on mean low water (MLW).

DESCRIPTION OF THE STUDY AREA

The coastal bay system of Maryland is contained within the borders of Worcester County. The system is subdivided for the purposes of this study into five subsystems. These include, north to south: 1. Assawoman Bay (north of the eastern segment of the Maryland State Route [MDSR] 90 bridge extending to the Maryland-Delaware state line); 2. Isle of Wight Bay system, south of both segments of the MDSR 90 bridge to the north side of the US 50 bridge, whose principle tributary is the St. Martins River which extends north of the western segment of the MDSR 90 bridge, and the minor tributaries of Herring Creek, Turville Creek, and Manklin Creek; 3. Sinpuxent Bay which includes, at the north end, Ocean City Inlet south of the US 50 bridge to the West Ocean City Commercial harbor south to South Point; 4. The Ayre Creek/Trappe Creek/Newport Bay system; 5. Chincoteague Bay (from South Point south to the Maryland Virginia state line); and 6. The nearshore of the Atlantic Ocean. Estimates of the surface acreage of the coastal bay systems were published by Counts et al. (1992) who reported Assawoman Bay to have a surface acreage of 5,837 acres (2,364 ha), the St. Martins River system 1,984 (803 ha), Isle of Wight Bay and associated tributaries 7,494 acres (3,035 ha), Ocean City Inlet 224 acres (91 ha), Sinpuxent Bay 5,813 acres (2,354 ha), Ayre Creek/Trappe Creek/Newport Bay system 4,258 acres (1,724 ha), and Chincoteague Bay at 47,229 acres (19,128 ha) for a total coastal bays system acreage of 72,839 acres (29,499 ha). Biggs (1970) reported the entire area of Chincoteague Bay as 428 km².

Assawoman Bay averages between 0.6 and 0.9 m deep along the shore with a deeper (1.2 to 2.1 m) central channel. The St. Martins River system also has shallow shore waters but averages mid-channel depths of 1.5 to 1.8 m

beginning at Saint Martins by the Bay to the MDSR 90 bridge. Casey and Wesche (1982) reported salinities in this system to range from 25.5 to 27.1 parts per thousand (ppt).

Isle of Wight Bay is the largest areas of deepest coastal bay water (1.2 to 1.8 m) in the northern half of the coastal bays system with the majority of this deep water being located between the MDSR 90 bridge to a point approximately half the distance south to the US 50 bridge. The southern portion of the Isle of Wight Bay has shallow water with an extensive system of mud banks and shoals extending almost to the north edge of Ocean City inlet. The three creeks associated with Isle of Wight Bay (Manklin, Turville and Herring) are all extremely shallow with the deepest water (approximately 1.22 m) located between Cape Isle of Wight and Cotton Hill. Ocean City Inlet has a channel that is maintained at an average depth of 2.3 to 2.6 m and deepens to 3.1 m (United States Department of Commerce 2002). The average depth of Sinepuxent Bay ranges from 1.0 to 1.5 m with a 2 m channel that deepens as it approached Ocean City Inlet. The Ayre Creek/Trappe Creek/Newport Bay system depths range from < 1m at its head to 2 m at the juncture with Chincoteague Bay. Biggs (1970) reported the average width of Chincoteague Bay to be 11.9 km with an average depth ranging between 1 and 3 m deepening to 28 m at Chincoteague Inlet, Virginia. Salinities in the Isle of Wight Bay system range from 21.0 to 26.2 ppt in the Herring Creek tributary, 25.0 to 27.0 in Turville Creek, and 24.0 to 30.0 ppt in the main body of Isle of Wight Bay (Casey and Wesche 1982).

Seiling (1954) described the physical characteristics of the Chincoteague-Sinepuxent Bay system and noted that in summer months, water temperatures are cooler at the Ocean City Inlet and warmer in the shallow bays. In winter, this pattern is reversed and occasionally the bays will freeze-over with ice. In summer, salinities were found to decrease toward the inlets where tidal surge mixes seawater with high salinity bay waters. Summer salinity patterns result from a net water loss from evaporation that is made up by tidal inflow and a minimal freshwater inflow from freshwater streams of the mainland (Seiling 1954; Pritchard 1960; Pellenbarg and Biggs 1970). Data collected in 1989 indicated a higher than usual rainfall and salinities in Chincoteague Bay ranged from 27 to 29 ppt, the highest measurements being near the inlets. Counts and Prezant (2002) reported salinities in Sinepuxent Bay that ranged annually from 31.5 to 35.0 ppt nearest Ocean City Inlet and between 27.0 to 33.8 ppt where

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Sinepuxent Bay joins Chincoteague Bay: a salinity measurement taken at this juncture in October 2007 was 42.0 ppt.

Tidal amplitudes are not dramatic in the Maryland coastal bays or mid-Atlantic coast. Amplitude in Ocean City is approximately 1 m and the amplitude of the bays is about 0.33 m. The currents in Chincoteague and Sinepuxent bays are mostly independent of the non-oceanic currents and water flows away from the inlets at Ocean City and Chincoteague as the tide rises (Pellenbarg and Biggs, 1970). Bay water circulation is such that the tidal water movement of the bays allows a daily water exchange of approximately 7.5% from oceanic sources (Pritchard, 1960). Pellenbarg and Biggs (1970) reported Chincoteague and Sinepuxent bays to be essentially stagnant and intensely heated during the summer months. Sieling (1954) noted that the currents throughout these bays, although of no great magnitude, may have some influence on fin and shellfish distribution. Counts and Prezant (2002) reported water temperatures along the bay shores of Assateague Island to range from 7.4° - 15.0°C in spring; 16.8° to 32.8°C in summer; and 7.8° to 10.0°C in fall.

Bartberger (1976) noted that the sediments of Sinepuxent Bay are almost 100% sand decreasing to 80 to 90% sand in the dredged channel. In Chincoteague Bay, high percentage sand sediments are restricted to bottoms in the center of the bay become less sandy (down to 20 to 40% sand) along the Assateague Island shore and even lower (0 to 20% sand along the mainland coast. These low percentage sand sediments account for approximately 50% of the bottom of Chincoteague Bay and nearly 100% of the Newport Bay/Ayre Creek/Trappe Creek system. Bartberger (1976) also reported that approximately 90,000 m³ of sediments are transported into Chincoteague Bay every year. Maurmeyer (1981) noted that the reason the bay does not fill at these rates of sedimentation is that sea level rise has kept pace with sedimentation.

Darmody and Foss (1978) estimated the total acreage of coastal marshes in Worcester County to be 18,306 acres (7,322.4 ha). The figure accounted for 95% of the total marshes within the county. Foss (1981) also reported that almost the entire coast associated with the coastal bays systems were coastal saline marshes. McCormick and Somes (1982) reported 9,544 acres (3,817.6 ha) of seaside marshes in Worcester County which comprised an estimated 69.4% of total saline wetlands. They noted that 95 acres (30.0 ha) of these wetlands located along the margins of bays and channels were vegetated by *Spartina alterniflora* growing to a height of 2(0.6 m) to 4 ft (1.2 m) with shorter cordgrass growing

behind this tall grass margin. Spaur et al. (1998) estimated a historic area of coastal marshes to be 7,450 ha with 800 ha lost to development for a total loss of 115 ha. Their study indicated the greatest loss was along the coastal bays north of Ocean City Inlet (600 ha lost), as compared to those bays south of the inlet (111 ha lost). Chambers (1990) reported Maryland (Worcester County) was losing 1,000 acres (404.6 ha) yr^{-1} of coastal marshes: a rate that was slowed to a loss of 20 acres (8.09 ha) year^{-1} after the passage of wetlands protection legislation. Allison (1974) estimated that nearly one-quarter of all marshland on the fringes of Assawoman Bay had been lost to development. There are no known comparative studies delineating the change in salt marsh area attributable to development, sea level rise, or combinations of these and other factors (Counts and Jesien 2008).

Orth et al. (1986) mapped the submerged aquatic vegetation (SAV) of Chincoteague – Sinepuxent bays and reported 2,134 hectares of bottom having moderate (40 to 70%) to dense (70 to 100%) coverage. SAV species found were *Zostera marina* (dominating in the southern half of Chincoteague Bay) and *Ruppia maritima* (dominating the northern half of Chincoteague Bay). All SAV was found west of Assateague Island on the eastern side of Chincoteague Bay in water less than 1 m. The beds are readily visible during aerial fly-overs of the lower coastal bays (Counts et al. 1992). SAV beds are now flourishing in Isle of Wight Bay just south of the MDSR 90 bridge and adjacent to Ocean City.

RESULTS

Forty-seven species in the Order Decapoda, distributed among 2 suborders, in 20 families and 31 genera have been reported for the Atlantic coastal waters of Maryland (Table 1). The Maryland Atlantic coastal bays were found to have a richer species diversity when compared to the faunas of Chesapeake and Delaware bays which had a reported 30 and 23 species, respectively (Lippson and Lippson 1997; Watling and Maurer 1973). Seventeen species of decapod Crustacea were common to all three systems but only *Sesarma reticulatum* and *Pinothores ostreum* were reported in only Chesapeake and Delaware bays (Table 2).

A comparison of the number of taxa reported in the Maryland coastal bays in the studies reviewed and collated revealed that the studies of Cargo (1958, 1959) reported the presence of six crab species that are generally of commercial importance (Table 3). Drobeck et al. (1970) reported only two species of decapods in their baseline study of invertebrates of the newly-established

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Assateague Island National Seashore and the companion baseline study devoted to Decapoda of the park by Leber and Lippson (1970) listed 20 species. Counts and Prezant (2002) reported the presence of 26 decapod species in the intertidal and just subtidal waters surrounding the Maryland portion of Assateague Island National Seashore. *Callinectes sapidus* was the only species of decapod Crustacea reported by all historical studies (Table 3).

Table 1. Systematic List of Decapod Crustacea found in Maryland Atlantic coastal waters.

Class Crustacea

Order Decapoda

Suborder Natantia

Section Penaeidea

Family Penaeidae

Penaens aztecus aztecus Ives, 1891

Penaens setiferus (Linné, 1758)

Section Caridea

Family Ogyrididae

Ogyrides alphaerostris (Kingsley, 1880)

Family Palaemonidae

Palaemonetes intermedius Holthuis, 1949

Palaemonetes pugio Holthuis, 1949

Palaemonetes vulgaris (Say, 1818)

Family Hippolytidae

Eualus gaimardii (H. Milne Edwards, 1837).

Hippolyte pleuracanthus (Stimpson, 1871)

Hippolyte zostericola (Smith, 1873)

Family Crangonidae

Crangon septemspinosa Say, 1818

Sabinea sarsii Smith, 1879

Sabinea septemcarinata (Sabine, 1824)

Family Alpheidae

Alpheus heterochaelis Say, 1818

Suborder Repantia

Section Macrura

Family Callinassidae

Callinassa atlantica Rathbun, 1926

Family Upogebiidae

Upogebia affinis (Say, 1818)

Section Anomura

Family Pocellanidae

Enceramus praelongus Stimpson, 1860

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Table 1. Continued.

	<i>Pagurus acadianus</i> Benedict, 1901
	<i>Pagurus longicarpus</i> Say, 1817
	<i>Pagurus pollicarus</i> Say, 1817
	Family Hippidae
	<i>Emerita talpoida</i> (Say, 1817)
Section Brachyura	
	Family Hepatidae
	<i>Hepatus epheliticus</i> (Linné, 1763)
	Family Majidae
	<i>Libinia dubia</i> H. Milne Edwards, 1834
	<i>Libinia emarginata</i> Leach, 1815
	Family Portunidae
	<i>Arenaeus cribrarius</i> (Lamarck, 1818)
	<i>Callinectes sapidus</i> Rathbun, 1896
	<i>Callinectes sinuatus</i> Williams, 1966
	<i>Carcinus maenas</i> (Linné, 1758)
	<i>Ovalipes ocellatus</i> (Herbst, 1799)
	<i>Portunus gibbesii</i> (Stimpson, 1859)
	<i>Portunus spinimanus</i> Latreille, 1819
	Family Cancridae
	<i>Cancer borealis</i> Stimpson, 1859
	<i>Cancer irroratus</i> Say, 1817
	Family Varunidae
	<i>Hemigrapsus sanguinea</i> (de Haan, 1835)
	Family Xanthidae
	<i>Dyspanopeus sayi</i> (Smith, 1869)
	<i>Eurypanopeus depressus</i> (Smith, 1869)
	<i>Hexapanopeus angustifrons</i> (Benedict and Rathbun, 1891)
	<i>Neopanope texana</i> (Smith, 1869)
	<i>Panopeus herbstii</i> H. Milne Edwards, 1834
	<i>Rhithropanopeus harrisii</i> (Gould, 1841)
	Family Pinnotheridae
	<i>Pinnixa clatopseana</i> Stimpson, 1860
	<i>Pinnixa cylindrica</i> (Say, 1818)
	<i>Pinnixa sayana</i> Stimpson, 1860
	Family Grapsidae
	<i>Sesarma ciuereum</i> (Bosc, 1802)
	<i>Sesarma reticulatum</i> (Say, 1817)
	Family Ocypodidae
	<i>Ocypode quadrata</i> (Fabricius, 1787)
	<i>Uca pugilator</i> (Bosc, 1801 or 1802)
	<i>Uca pugnax</i> (Smith, 1870)

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Table 2. Comparison of species of decapod Crustacea present in the coastal bays of Maryland with those reported for Delaware Bay (Watling and Maurer, 1978) and Chesapeake Bay (Lippson and Lippson, 1997).

Species	Maryland Coastal Bays	Delaware Bay	Chesapeake Bay
<i>Penaeus aztecus</i>	+	+	-
<i>Penaeus duorarum</i>	-	-	+
<i>Penaeus setiferus</i>	+	-	+
<i>Ogyrides alapharostris</i>	+	-	-
<i>Palaemonetes intermedius</i>	+	-	-
<i>Palaemonetes pugio</i>	+	+	+
<i>Palaemonetes vulgaris</i>	+	-	-
<i>Eualus gainardii</i>	+	-	-
<i>Hippolyte pleuracanthus</i>	+	-	-
<i>Hippolyte zostericola</i>	+	-	-
<i>Crangon septemspinosa</i>	+	+	-
<i>Sabinea sarsii</i>	+	-	-
<i>Sabinea septemcarinata</i>	+	-	-
<i>Alpheus heterochaelis</i>	+	-	-
<i>Homarus americanus</i>	+	+	-
<i>Callinassa</i> sp.	-	+	-
<i>Callinassa atlantica</i>	+	-	-
<i>Upogebia affinis</i>	+	+	+
<i>Euceramus praelongus</i>	+	-	-
<i>Pagurus longicarpus</i>	+	+	+
<i>Pagurus acadianus</i>	+	-	-
<i>Pagurus annulipes</i>	-	+	-
<i>Pagurus pollicaris</i>	+	+	+
<i>Emerita talpoida</i>	+	+	+
<i>Hepatus epheliticus</i>	+	-	-
<i>Libinia dubia</i>	+	+	+
<i>Libinia emarginata</i>	+	+	+
<i>Arenaeus cribrarius</i>	+	-	-
<i>Callinectes sapidus</i>	+	+	+
<i>Callinectes similis</i>	+	-	-
<i>Carcinus maenas</i>	+	+	-
<i>Ovalipes ocellatus</i>	+	+	+
<i>Portunus gibbesii</i>	+	-	-
<i>Portunus spinimanus</i>	+	-	-
<i>Cancer irroratus</i>	+	+	+
<i>Cancer borealis</i>	+	+	-

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Table 2. Continued.

Species	Maryland Coastal Bays	Delaware Bay	Chesapeake Bay
<i>Hemigrapsus sanguinea</i>	+	-	-
<i>Eurypanope depressus</i>	+	+	+
<i>Hexapanopeus angustifrons</i>	+	-	-
<i>Dyspanopeus sayi</i>	+	+	-
<i>Neopanope texana</i>	+	+	-
<i>Panopeus herbsti</i>	+	+	+
<i>Rhithropanopeus harrisi</i>	+	+	+
<i>Pinnotheres ostreum</i>	-	+	+
<i>Pinnixa chaetoptera</i>	+	-	+
<i>Pinnixa cylindrica</i>	+	-	-
<i>Pinnixa retinens</i>	-	+	-
<i>Pinnixa sayana</i>	+	+	-
<i>Ocypode quadrata</i>	+	+	+
<i>Uca minax</i>	-	+	+
<i>Uca pugnax</i>	+	+	+
<i>Uca pugilator</i>	+	+	+
<i>Sesarma cinereum</i>	+	+	+
<i>Sesarma reticulatum</i>	-	+	+
<i>Euceramus praelongus</i>	+	-	-

Data presented in Table 4 indicate that decapod crustacean diversity decreased along a south to north line. The most diverse coastal bay segment was southernmost Chincoteague Bay with 34 species of Decapoda being reported, followed by the adjacent Sinepuxent Bay, with 30 species, and followed by Isle of Wight Bay with 15 species and Assawoman Bay with 11 species. The Newport Bay/Trappe Creek segment, which empties into Chincoteague Bay next to its confluence with Sinepuxent Bay, was the least diverse system and was reported to contain four species of decapod crustaceans present. Ten species of Decapoda were reported from the littoral of Maryland's Atlantic Ocean.

Bray-Curtis similarity indices for each segment of Maryland's coastal bays (Table 5) indicated that there was very little similarity between coastal bay decapod fauna and that of the Atlantic littoral. The indices indicate that the decapod fauna composition of each bay segment shows greatest similarity with that of the neighboring segment (e.g., Assawoman Bay and Isle of Wight Bay;

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Isle of Wight Bay with Sinepuxent Bay; and Sinepuxent Bay with Chincoteague Bay). There was little faunal similarity between the coastal bay segments separated by the greatest distance (Assawoman Bay and Chincoteague Bay).

Table 3. Species of decapod Crustacea collected in coastal waters of Maryland by investigations. (1) Cargo A=1958, B=1959. (2) Drobeck et al., 1970. (3) Leber and Lippson 1970. (4) Casey and Wesche, 1982 and other Maryland Department of Natural Resources reports. (5) Chaillou and Weisberg, 1996. (6) Counts and Prezant 2002.

Species	STUDY					
	1	2	3	4	5	6
<i>Penaeus aztecus aztecus</i>	-	-	-	+	+	-
<i>Penaeus setiferus</i>	-	-	-	+	-	-
<i>Ogrydes alphaerostris</i>	-	-	-	-	+	-
<i>Palaemonetes intermedius</i>	-	-	+	-	-	+
<i>Palaemonetes pugio</i>	-	-	+	+	+	+
<i>Palaemonetes vulgaris</i>	-	-	+	+	-	+
<i>Eualus gaimardii</i>	-	-	-	-	-	+
<i>Hippolyte pleuracanthus</i>	-	-	-	-	-	+
<i>Hippolyte zostericola</i>	-	-	-	-	-	+
<i>Crangon septemspinosa</i>	-	-	+	+	+	+
<i>Sabinea sarsii</i>		-	-	-	-	-
<i>Sabinea septemcarinata</i>	-	-	-	-	-	+
<i>Alpheus heterochaelis</i>	-	-	-	+	-	-
<i>Callinassa atlantica</i>	-	+	-	+	-	-
<i>Upogebia affinis</i>		-	-	-	-	+
<i>Eucramus praelongus</i>	-	-	-	-	-	+
<i>Pagurus acadianus</i>	-	-	-	-	-	+
<i>Pagurus longicarpus</i>	-	-	+	+	-	+
<i>Pagurus pollicarus</i>	-	-	+	+	-	-
<i>Emerita talpoida</i>		-	-	+	-	-
<i>Hepatus epheliticus</i>	-	-	-	+	-	-
<i>Libinia dubia</i>		-	-	+	+	-
<i>Libinia emarginata</i>	-	-	+	+	-	+
<i>Arenaeus cribrarius</i>	-	-	-	-	-	+
<i>Callinectes sapidus</i>	B	+	+	+	+	+
<i>Callinectes similis</i>	-	-	-	+	-	-
<i>Carcinus maenas</i>	-	-	-	+	-	+
<i>Ovalipes ocellatus</i>	-	-	+	+	+	+
<i>Portunus gibbesii</i>	-	-	-	+	+	+
<i>Portunus spinimanus</i>	-	-	-	+	-	-
<i>Cancer borealis</i>		-	-	-	-	-
<i>Cancer irroratus</i>		-	-	+	+	-

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Table 3. Continued

Species	STUDY					
	1	2	3	4	5	6
<i>Hemigrapsus sanguinea</i>	-	-	-	+	-	-
<i>Dyspanopeus sayi</i>	A	-	-	+	-	-
<i>Eurypanopeus depressus</i>	A	-	+	-	-	-
<i>Hexapanopeus angustifrons</i>	A	-	+	-	-	-
<i>Neopanope texana</i>	A	-	+	+	-	-
<i>Panopeus herbstii</i>	A	-	+	+	-	-
<i>Rhithropanopeus harrisi</i>	-	-	+	+	-	-
<i>Pinnixa chaetoptera</i>	-	-	-	-	-	+
<i>Pinnixa cylindrica</i>	-	+	-	-	-	-
<i>Pinnixa sayana</i>	-	-	-	-	-	-
<i>Sesarma cinereum</i>	-	-	-	-	-	+
<i>Ocypode quadrata</i>	-	-	+	-	-	+
<i>Uca pugilator</i>	-	-	-	+	-	-
<i>Uca pugnax</i>	-	-	-	+	-	-

Table 4. Species of decapod Crustacea collected in coastal waters of Maryland by body of water of occurrence. Atlantic Ocean (ATL), Assawoman Bay (AWM), Isle of Wight Bay (IOW), Sinepuxent Bay (SIN), Newport Bay/Trappe Creek system (NPT), and Chincoteague Bay (CHN).

Species	Body of Water					
	ATL	AWB	IOW	SPB	NTC	CHB
<i>Penaeus aztecus aztecus</i>	-	+	+	+	-	+
<i>Penaeus setiferus</i>	-	+	+	+	-	+
<i>Ogyrides alphaerostris</i>	-	+	+	-	-	+
<i>Palaemonetes intermedius</i>	-	-	-	+	-	+
<i>Palaemonetes pugio</i>	-	-	-	-	-	+
<i>Palaemonetes vulgaris</i>	-	-	+	+	-	+
<i>Eualus gaimardii</i>	-	-	-	+	-	+
<i>Hippolyte pleuracanthus</i>	-	-	-	+	-	+
<i>Hippolyte zostericola</i>	-	-	-	-	-	+
<i>Crangon septemspinosa</i>	-	-	+	+	-	+
<i>Sabinea sarsii</i>	-	-	-	-	-	+
<i>Sabinea septemcarinata</i>	-	-	-	-	-	+
<i>Alpheus heterochaelis</i>	-	+	+	+	-	+
<i>Callinassa atlantica</i>	-	-	-	+	-	+
<i>Upogebia affinis</i>	-	-	-	-	-	+
<i>Euceramus praelongus</i>	+	-	-	-	-	-

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Table 4. Continued

Species	Body of Water					
	ATL	AWB	IOW	SPB	NTC	CHB
<i>Pagurus acadianus</i>	+	-	-	-	-	-
<i>Pagurus longicarpus</i>	-	-	+	+	-	+
<i>Pagurus pollicarius</i>	+	-	-	+	-	-
<i>Emerita talpoida</i>	A	-	-	-	-	-
<i>Hepatus epheliticus</i>	-	+	+	+	-	+
<i>Libinia dubia</i>	-	-	-	+	-	+
<i>Libinia emarginata</i>	-	-	-	+	-	-
<i>Arenaeus cribrarius</i>	-	-	-	+	-	+
<i>Callinectes sapidus</i>	+	+	+	+	+	+
<i>Callinectes similis</i>	-	+	+	+	+	+
<i>Carcinus maenas</i>	-	B	-	+	-	-
<i>Ovalipes ocellatus</i>	+	+	+	+	+	+
<i>Portunus gibbesii</i>	-	+	+	+	-	+
<i>Portunus spinimanus</i>	-	+	+	+	-	+
<i>Cancer borealis</i>	+	-	-	-	-	-
<i>Cancer irroratus</i>	+	-	-	+	-	+
<i>Hemigrapsus sanguinea</i>	+	-	-	+	-	-
<i>Dyspanopeus sayi</i>	-	-	-	-	-	+
<i>Eurypanopeus depressus</i>	-	-	-	-	-	+
<i>Hexapanopeus angustifrons</i>	-	-	-	-	-	+
<i>Neopanope texana</i>	-	-	-	-	-	+
<i>Panopeus herbstii</i>	-	-	-	-	-	+
<i>Rhithropanopeus harrisi</i>	-	-	-	-	-	+
<i>Pinnixa chaetopterana</i>	-	-	-	+	-	-
<i>Pinnixa cylindrica</i>	-	-	-	+	-	+
<i>Pinnixa sayana</i>	-	-	-	+	-	-
<i>Searma cinereum</i>	-	-	-	+	-	-
<i>Ocypode quadrata</i>	+	-	-	+	-	-
<i>Uca pugilator</i>	-	-	-	+	+	+
<i>Uca pugnax</i>	-	-	-	+	+	+

(A) Records of Leber and Lippson (1970) and Weissman (1990)

(B) Tom Patton, personal communication, 2002.

Dendrograms for Bray-Curtis similarities between Maryland's coastal bays and Delaware and Chesapeake bay faunas are depicted in Fig. 2 along with similarities between segments of Maryland's coastal bay system.

DISCUSSION

The number and diversity of species reported by the various historical studies (Table 3) show differences for a variety of reasons that fall into a variety of categories. These include: 1) specificity and goals of the research program, 2)

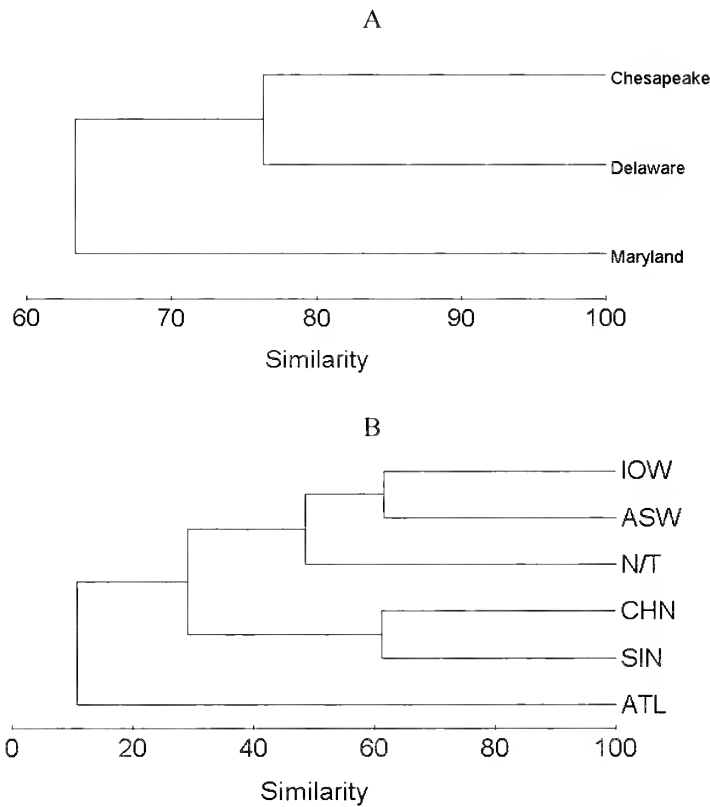


Fig. 2. Similarity dendrograms: A: similarity between decapod Crustacea fauna of Maryland's Atlantic coastal bays and Delaware and Chesapeake bays. B: similarity between decapod crustacean fauna of Maryland Atlantic coastal waters (CHN = Chincoteague Bay, SIN = Sinepuxent Bay, IOW = Isle of Wight Bay, AWM = Assawoman Bay, NPT = Newport Bay-Trappe Creek system, ATL = Atlantic Ocean).

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sampling protocol and gear usage, 3) duration of study, 4) time of year of sampling, 5) year of sampling, and 6) site and geographic variation. Some studies were targeted towards a particular biota. For example, Cargo (1954, 1955, 1959) was chiefly concerned with decapods that have commercial importance. Leber and Lippson (1970) examined only Sinepuxent and Chincoteague bays as

Table 5. Bray-Curtis similarity matrix calculated from the presence or absence of decapod crustacean species in Maryland Coastal Bay segments. ATL = Atlantic Ocean; AWB = Assawoman Bay, IOW – Isle of Wight Bay, SPB = Sinequxwent Bay, NTC = Newport Bat/Trappe Creek, CHB = Chincoteague Bay.

	ATL	AWB	IOW	SPB	NTC	CHB
ATL		•	•	•	•	•
AWB	10.000					
IOW	16.667	84.615	16.667		•	
SPB	25.641	98.780	62.222			•
NTC	14.286	37.500	30.000	28.571		•
CHB	13.636	43.478	56.000	70.789	25.000	
% Similarity						
10 - 30	•	30 - 60		60 - 90		>90

their study was designed to provide a baseline survey of decapod crustaceans in those waters behind the newly-established Assateague Island National Seashore. Drobeck et al. (1970), while contemporaneous with Leber and Lippson devoted their studies to invertebrates other than the Decapoda and the two species they mentioned were incidental to their findings. Similarly, Counts and Prezant (2002) studied the fauna of the waters in Sinepuxent and Chincoteague bays but also examined the Atlantic littoral of the national seashore and their study was seasonal over a two-year period. The studies of Casey and Wesche (1982), and other reports by them and colleagues, are devoted to the entire coastal bays system and cover an extended period of time. Chaillou and Weisberg (1995), while covering the entire system with an extensive number of samples, did not identify many of the decapods collected below the level of genus. These studies of only portions of the coastal bay system, coupled with changes in taxonomy, and incomplete identifications, have caused some confusion.

For example, Chaillou et al. (1996) reported collecting members of the genus *Pinnixa* in Assawoman Bay but did not identify their specimens to the species level. Abele (1972) reevaluated the *Neopanope texana-sayi* complex and concluded, based on the examination of types and other material, that both are distinct species allopatric in distribution: *N. texana* occurring in the Gulf of Mexico and *N. sayi* occurring along the east coast of North America. Although Cargo (1959) reported the occurrence of *Neopanope texana* in Chincoteague Bay, it is believed this represents *Dyspanopeus sayi*. Casey and Wesche (1982) believed they recognized both species and the reports of the occurrence of *N. texana* could represent an importation of a Gulf species into Maryland's coastal bays such as that of the Florida drill, *Stramonita haemastoma floridana* (Conrad, 1837) (Mollusca: Gastropoda) into the Chincoteague Bay area of Maryland and Virginia. Here dredged shells indicated that the species was established at a much earlier date in the Maryland part of Chincoteague Bay, perhaps before the closure of the Green Run inlet in 1883 (Sieling 1960; Prezant et al. 2002).

The *Callinectes sapidus* fishery of Chincoteague Bay has long been the subject of investigation (Chesapeake Biological Laboratory 1944, 1947; Cargo and Cronin 1951; Anonymous 1955; Cargo 1954, 1955; Casey 1995; McConaugha 1999; Wesche 1999) and regulations of the fishery were examined for efficacy (Cronin 1944, 1947). The biology of the species has been examined for migration patterns of female *C. sapidus* of Chincoteague Bay (Cargo 1959); epizootic infection by *Paramoeba perniciosus* (Newman and Ward 1973); bacterial infections of the hemolymph (Tubiash et al. 1975; Johnson 1976); *Hematodinium perezii* infections in adult and juvenile (Messick 1994); virus-like infections (Rosenfield 1976); genetic variability between populations in Chesapeake Bay and Chincoteague Bay (Cole and Morgan 1978); and recruitment and growth (Anderson and Van Heukelem 1995).

The increased diversity in decapod crustacean species observed as one moves from north to south in the Maryland coastal bay system may be attributable to a relative decrease in human impacts on these bodies of water as one moves in that direction. Assawoman Bay and Isle of Wight Bay, located north of Ocean City Inlet, have shores with a high degree of commercial and residential development while Sinpuxent and Chincoteague bays, located south of the inlet, are relatively undeveloped on their western shore and completely undeveloped on their eastern shores due to the presence of the National Seashore.

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Physicochemical characteristics of the coastal bay system components may also account for the distributional patterns observed for Decapoda. Wazniak et al. (2004a) noted that total nitrogen measurements were lowest in Sinepuxent and Chincoteague bays and that the upper tributaries of the northern segments and the Newport Bay system were severely eutrophic. They further noted that phosphorus enrichment was more diffuse throughout the coastal bays but that levels of this nutrient sufficient for seagrass bed growth could be found in Sinepuxent and Chincoteague bays. Wazniak et al. (2004b) also reported that daytime measurements of dissolved oxygen concentrations were frequently below 5 mg L^{-1} in the St. Martin's River, Herring and Turville creeks, the Newport Bay system and portions of Chincoteague Bay. They also noted that dissolved oxygen levels were below 5 mg L^{-1} 40% in 60% of their measurements made in the tributaries but less so in the open bays (Wazniak et al. 2004b). Carruthers and Wazniak (2004) reported that of six sites monitored in Assawoman Bay had degraded water quality due principally to high nutrient inputs of total nitrogen and total phosphorus. They reported that while the Isle of Wight Bay proper had good water quality, the tributaries were degraded or poor. Carruthers and Wazniak (2004) summarized that the coastal bays generally had poor water quality in or near tributaries but quality was judged to be excellent in Sinepuxent and southern Chincoteague bays and stated that variations in water quality reflected variations in nutrient concentrations, high phytoplankton concentrations or reduced dissolved oxygen. Wells and Hill (2004) reported that sediment chemical contamination levels were low throughout the southern coastal bays and the open water of the northern bay segments but were high in localized areas of bay tributaries and the Newport Bay system.

Salinity concentrations can serve as apparent cues to trigger metamorphosis of larval stages of Decapoda and may account for the observed distribution of the species in Maryland's coastal bays. These salinity effects have been described and reviewed for many of the species present on the Maryland coast (Christy, 1989; O'Connor, 1991; Forward et al., 1994, 1996, 1997; Wolcott and DeVries, 1995; Weber and Epifanio, 1996; O'Connor and Gregg, 1998; and Rodriguez and Epifanio, 2000; Gebauer et al., 2003). Of these studies, Forward et al. (1994, 1996, 1997) and Wolcott and DeVries (1995) reported that decreased salinity of estuarine water to be a cue for metamorphosis in *Callinectes sapidus*. None of the other decapod species found in the Maryland coastal bays that were examined in these studies (*Panopeus berbstii*, *Uca pugilator*, and *Uca pugnax*)

demonstrated a salinity-related cue to metamorphosis. Cues for metamorphosis have been variously identified as presence of adult odors in the water column (O'Connor, 1991); presence of seagrass, macroalgae, *Ulva latuca*, *Uca rotundata*, *Bryophyta plumulosa*, and *Hypnea musciformis* (Forward et al., 1996); presence of *Fucus vesiculosus*, rock and shell or other substrata (Weber and Epifanio, 1996; Dittel et al., 1996); presence of adults (O'Connor and Gregg, 1998; Rodriguez and Epifanio, 2000). Rodriguez and Epifanio (2000) further reported that the presence of *Dyspanopeus sayi* is a cue for metamorphosis in *Panopeus herbstii* in laboratory experiments.

Human use and impacts can also have an effect on decapod crustacea. On the Atlantic coast, Weissman (1994) examined environmental variables affecting the population density of the mole crab, *Emerita talpoida* Say, 1822 along the barrier island coast of Maryland and found that density differences could be detected for beaches with the highest and lowest human disturbance, although she found no linear relationship, and that beach replenishment and pedestrian traffic are the most effective types of human disturbance. She further noted that off road vehicle traffic had no visible effect on crab density, while season had the greatest effect on crab population density. This was consistent with the findings of Steiner and Leatherman (1981) and Christoffers (1987) who examined recreational impacts on distribution of *O. quadrata* at Assateague Island, Maryland-Virginia. They found that off-road vehicles (ORV) and pedestrian-impacted beaches, could be adversely affecting the crabs directly by crushing or burying them or indirectly by interfering with their reproductive cycle or altering their environment. Pedestrians appeared to have no harmful effects on crabs which may have capitalized on the food scraps scattered across the beach by bathers. We cannot offer any hard evidence for any human disturbance on decapods on the Assateague Island beaches due to the relatively shallow sampling (Counts and Prezant 2002).

Although the exotic species *Hemigrapsus sanguinea* and *Carcinus maenas* are now present in limited numbers in the Atlantic coastal bay system of Maryland, no study of their impact upon the endemic decapod fauna has yet been conducted.

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THE EARLIEST RECORDS OF LAND SNAILS IN MARYLAND:
THE REVEREND HUGH JONES, MARYLAND'S FIRST FIELD
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ABSTRACT

Four species of land snails (Gastropoda: Pulmonata) were collected in the Maryland Colony in 1697 by the Reverend Mr. Hugh Jones, Pastor of Christ Church in Calvert County, and were sent with other specimens to James Petiver, F.R.S., in London who described the species in a paper published in the Philosophical Transactions of the Royal Society. The species are identifiable as *Neohelix albolabris*, *Anguspira alternata*, *Mesodon thyroidus* and *Triodopsis tridentata*.

INTRODUCTION

The Reverend Hugh Jones (1671-1702) is a difficult man to pin down in the history of Maryland. There were no less than four Reverend Joneses living in and about the state from the late 1690s to 1720s (Landrum, 1943). Indeed, several early works describing these men confuse and mix their biographies and accomplishments (e.g., Adams, 1887; Landrum, 1943; Morton, 1950).

Hugh Jones was born in 1671, the son of Thomas Jones, at Llanedwin in County Merioneth, northwest Wales. On 15 November 1694, he and three other young men matriculated at Gloucester Hall, a divinity school that was a part of Oxford University; Jones as a pauper student (Landrum, 1943). By the time of his

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matriculation, Gloucester was in serious decline and it was a local joke that its real name was Rump Hall (after a local alehouse) (Kammen, 1963). Before and during his time at Gloucester Hall, he served as an assistant to Edward Lhwyed, Keeper of the Ashmolean Museum of Oxford (Kammen, 1963).

At this time, the Reverend Doctor Henry Compton, Bishop of London, was looking for a "Person in orders that may goe to Maryland to be ehaplain to Mr. (Francis) Nicholson," Governor of the colony. Maryland had originally been a part of the Virginia colony until Charles I gave a grant to Charles Calvert, Lord Baltimore, which he passed on to his son Cecil Calvert. It was Cecil who established the first colony in 1632 at Kent Island in Chesapeake Bay (Thompson, 1812). Despite 62 years of colonization, by the 1690s the only true town in the colony was Annapolis (Jones, 1699). Bishop Compton himself had an interest in botany so he was apparently delighted to receive young Mr. Jones who also had an interest in natural history and carried a letter of introduction from Lhwyed to that effect. After meeting with the bishop, Jones wrote to Lhwyed that Compton would send him to Maryland but he first had to post a £40 bond to insure he would indeed go to the colony in America. Once Compton had the bond in hand, he gave Jones £20 from the King's Bounty. Even though Jones was not ready for ordination by the standards of the day, he was made a deacon and admitted to holy orders as an Anglican priest (Kammen, 1963).

Jones set out for Maryland at The Downs in 1695 and there he boarded the ship *The John*. There were, however, many delays and it was during these that he met James Petiver (1665 – 1717), an Apothecary and Fellow of the Royal Society in London. Apothecaries were considered to the second tier of the medical establishment in England, the first being physicians and the last being surgeons (Armstrong, 1954). Petiver, who had a deep interest in natural history, particularly medicinal plants, had assembled a group of over 80 correspondents who sent him natural history objects from around the world (Stearns, 1953) and he recruited Jones into this group. Jones eventually sailed for Maryland from the Isle of Wight in May 1696. Upon his arrival in the colony, Jones met with Governor Nicholson and Annapolis. Instead of becoming the Governor's chaplain, however, Nicholson sent Jones to Calvert County to head the Christ Church Parish, which had 537 tithing members who annually contributed 21,480 pounds of tobacco worth approximately £100 (Kammen, 1963).

Once established in the parish, Jones began collecting plants, seeds, shells, fossils, and other animals. His activities became so time consuming that he

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eventually hired a collecting assistant to help with plants and fossils. By March 1697, Jones sent two boxes of materials back to Petiver in London, which he received in May 1697. One box contained plant material, including seeds, and the second contained the shells of four land snails, a turtle, a crab, and 13 insects (Petiver, 1698).

On 23 January 1699, Jones wrote to the Reverend Dr. Benjamin Wooddrosse, F.R.S., describing the physiography and geography of the Maryland colony (Jones, 1699). Although a portion of this letter was published in the *Philosophical Transactions* (Jones, 1699), the entire letter has been republished with annotations by Kammen (1963) and describes agricultural, forestry, meteorological, manufacturing, and governmental affairs of the colony as well as a brief description of Indian affairs. By 1700, Jones was in failing health with asthma (Kammen, 1963) and possibly tuberculosis (Olson, 2010). Jones had written that he was emotionally distressed as well as ill and stated that it was his intention to return to Wales the following year. By February 1701 he was too ill to continue collecting and stopped his expeditions. He died in January 1702, aged 30 years (Kammen, 1963).

James Petiver numbered among his friends Martin Lister and transmitted letters to the Society from such luminaries as Anthony van Leeuwenhock. His first published works in the *Philosophical Transactions of the Royal Society* works include a review of *Musei Petiveriani Centuria Prima. Rariora Naturae continens: viz Animalia, Fossilia, Plantas, ex variis Mundi plagis advecta, Ordine digesta, Nominibus propriis signata et Iconibus aeneis eleganter illustrata* by S. Smith; B. Walford (Petiver, 1697a) and a catalogue of some plants from Guinea (Petiver, 1697b).

JONES' GASTROPODS

Petiver (1698) reported the presence of four species of gastropods from Maryland that had been sent to him by the Reverend Hugh Jones. These he listed as land shells and were the third through sixth animals he described in the paper. While there are pictorial references to these gastropods, which appear in Lister's (1685) *Historiae Conchyliorum*, there is no mention of size, habitat, or specific locality other than "Maryland." This method of matching specimens to illustrations in shell books was a commonly accepted practice among naturalists before the Linnaean system was adopted in the late 18th century. Margócsy

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(2010) noted that during the 17th century numerous catalogues were published by naturalists. Martin Lister's *Historium Conchyliorum* (Lister, 1685) was precisely this type of book providing illustrations of shells arranged by their apparent relatedness and identified, if at all, by a cursory line or two of description. Many such books on conchology were produced most likely due to the extensive trade in exotic shells as they were probably the least troublesome natural history collectables; the shell itself was small, did not rot, and was easily transported (Margócsy, 2010). The references Petiver (1698) made to the *Historium Conchyliorum* were because, as noted by Margócsy (2010), it was the universally accepted authority for the trade of mollusc shells. Thus, the starting point for identification of the four species of land snails sent by Jones to Petiver begins with their illustrations in Lister (1685). The species reported by Petiver (1698) are as follows.

Neohelix albolabris (Say, 1816)

This first snail (and fourth animal) reported by Petiver (1698) was described as “*Cochlea terrestris major striatea, ore compresso. Cochlea Virginiana*” [a large terrestrial snail, striated with a compressed aperture]. Petiver then reported the animal was figured (fig. 45, *Cochlea Virginiana*) in Lister's *Historiae Conchyliorum* (Lister, 1685), which appears to be *Neohelix albolabris* (Fig. 1A). Say, (1818) stated the species was figured in Lister (1685) on plate 47 but did not know the figure number. Pilsbry (1940) identified the species as *Triodopsis albolabris* (Say, 1817), which he placed in the subgenus *Neohelix* (von Ihering, 1892) and began his synonymy with *Helix albolabris* (Say, 1816). The subgenus has since been revised placing *T. albolabris* in *N. albolabris*. Grimm (1971) reported the species from all of Maryland's counties and Hubricht (1985) reported the species (as *T. albolabris*) from every county in Maryland except Somerset and Worcester and reported he had collected the species on wooded hillsides and in ravines under logs on rocks and in leaf litter, along roadsides and railway beds as well as in urban settings. Örstan (1999) reported *N. albolabris* from Black Hill Regional Park, Montgomery County.

Anguispira alternata (Say, 1816)

The second snail Petiver reported from Maryland was described as “*Cochlea ter. Virginiana insigniter striata, umbilico magna. Cochlea umbilicata, fusca, sive variegata, capillaribus striis leviter exasperata.*” This snail was figured

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(fig. 69) in Lister's *Historiae Conchyliorum* (Lister, 1685) (Fig. 1B). The caption roughly translates to "Terrestrial snail shell from Virginia remarkable for furrows (striations), large umbilicus. Umbilicate snail shell, dusky, but variegated, elevated and depressed light roughened striations." The species name has a convoluted history beginning with Lister's figure and Petiver's description. Both Lister and Petiver predate Linné's *Systema Naturae*, 10th edition (1758), the taxon with priority should have been that for snails described by Müller (1774) as *Helix radiata*, albeit listed by him as a species from southern France. The specimen figured in Lister (1685) the description of Petiver (1698) were both cited by Müller but his locality probably accounts for confusion about the geographic origins of the snail. The snail was subsequently identified in Nicholson's encyclopedia (Say, 1819) as *Helix alternata* and in it he mentioned Lister's (1685) figure as well as repeated the caption that accompanied the figure. Binney and Bland (1869) noted that the species appeared in Nicholson's encyclopedia and preserved the genus *Helix*, listing *Anguispira alternata* Morse (1864) as a junior synonym. Pilsbry (1948) redescribed the species and his extensive synonymy began with Müller's (1774) partial description of *Helix radiata*.

The species is still common in the state; Grimm (1971) reported this species to be common on the Maryland coastal plain and that it occurred in Allegany, Baltimore, Calvert, Carroll, Cecil, Dorchester, Frederick, Garrett, Harford, Montgomery, Talbot, Washington, and Worcester counties and Baltimore City. Hubricht (1985) reported *A. alternata* from Allegany, Baltimore, Calvert, Carroll, Cecil, Dorchester, Frederick, Garrett, Harford, Howard, Montgomery, Prince George's, Talbot, Washington, and Worcester counties and noted the species could be found in a wide variety of habitats that included woodlands around logs, hollow trees, rocks, weedy roadsides, along railroads, and in vacant lots and gardens in urban settings. The latest report of the species in Maryland is by Norden (2008) who reported it at Plummers Island of the Potomac River.

Mesodon thyroideus (Say, 1818)

The third species was described "Cochlea terrestris Virginiana media umbilicata, striata, ore unidentate compresso. Cochlea umbilicata, capillaceis striis per obliquum donata, unico dente ad fundum oris." [Virginian snail shell umbilicus in the middle, striated, with one compressed tooth in the aperture.

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Umbilicate snail shell, hairy oblique striae throughout, single tooth at the bottom of the mouth (aperture)]. Petiver then stated the snail was figured (fig. 91) in Lister's *Historiae Conchyliorum* (Lister, 1685) (Fig. 1C). Say (1918) did not refer to Lister's (1685) figure but Férussac (1821) did, placing the snail in *Helix thyrroidus*. Pilsbry (1940) provided a synonymy for the species that began with *Helix thyrroidus* Say, 1817. The date of authorship is widely reported as 1816 but was cited as 1817 by Binney in his bibliography (1864) and his report was given great support by the research of Johnson (1974). Grimm (1971) and Hubricht (1985) reported the species to be ubiquitous in Maryland. The latest reports of the species in the state are by Örstan (1999) who reported *M. thyrroidus* from Black Hill Regional Park, Montgomery County and Norden (2008) who reported *M. thyrroidus* to be the most common large snail on Plummers Island.

Triodopsis tridentata (Say, 1816)

The fourth snail described in Petiver's 1698 paper was described as "Cochlea parva umbilicata, tenuiter striata, tridens, scil. in triangulo positi, nempe unus as fundum oris, alter as eolumellum, terius ad labrum." [Loosely translated as "Snail shell with minimal umbilicus, with drawn-out striations, three teeth, clearly in a triangular position, one always at the bottom of the mouth near the columella, the others on the lip." Petiver noted this species had been figured (fig. 92) in Lister's *Historiae Conchyliorum* (Lister, 1685) (Fig. 1D). Pilsbry (1894) reported *Triodopsis tridentata* (as *Polygyra tridentata*) from western Maryland but did not report the species in the state in his 1940 monograph. Grimm (1971) reported the species from Allegany, Cecil, Garrett, Harford, and Washington counties, the Cecil and Harford records being restricted to the Susquehanna River valley. Hubricht (1985) reported the snail from Allegany, Cecil, Garrett, Harford, and Washington counties.

These four species represent the first reported land snails from the colony of Maryland but not from the region or the Atlantic coast colonies. Petiver went on to describe other molluscs from Virginia, Maryland and the Carolinas in his *Gazophylacii Naturae* (Petiver, 1702) and another series of shells sent to him from the Carolinas (Petiver, 1705).

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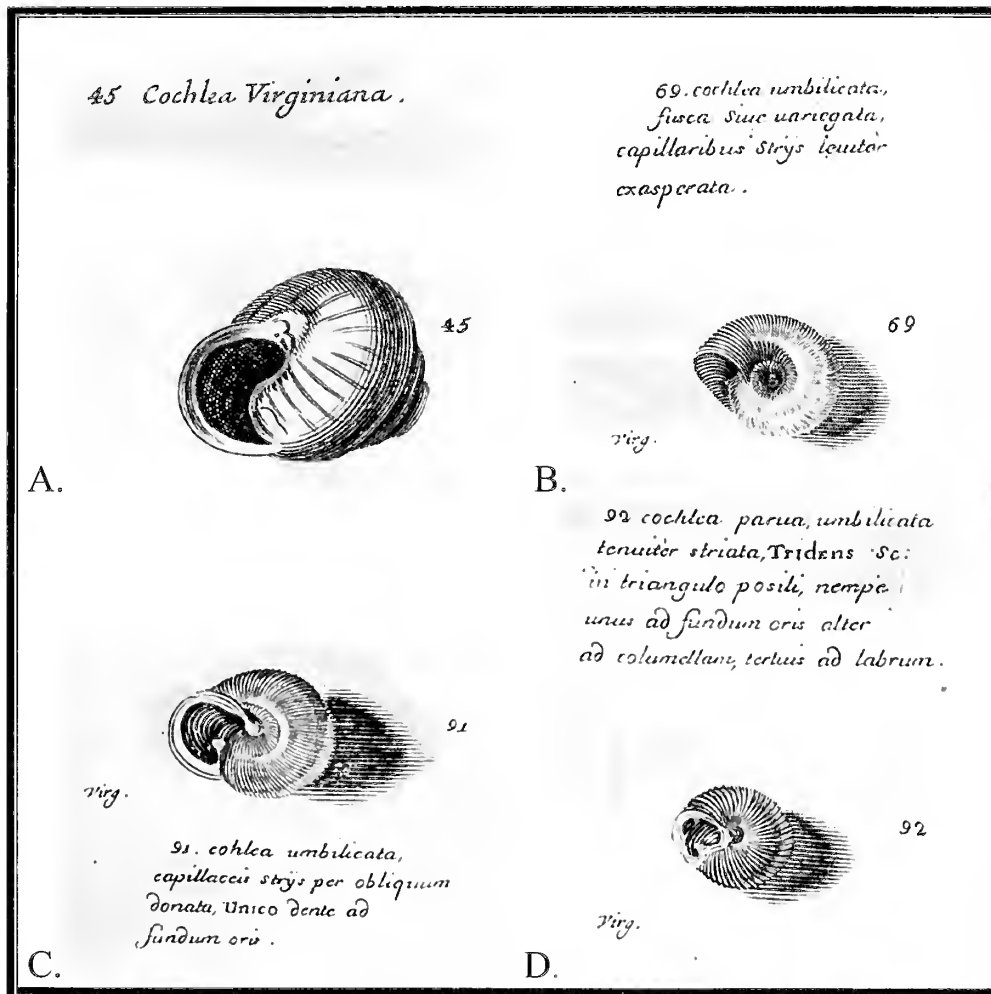


Figure 1. Illustrations from Lister's (1685) *Historiae Conchyliorum* referred to by Petiver (1689) in his description of land snails sent to him from Maryland by Hugh Jones. A = *Neohelix albolabris*; B = *Anguispira alternata*; C = *Mesodon thyroidus*; and D = *Triodopsis tridentata*.

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